ECOLOGICAL DIFFERENTIATION IN SOME CONGENERIC SPECIES OF COSTA RICAN FLOWERING PLANTS[1]

WILLIAM C. BURGER[2]

Initial work for a new flora of Costa Rica disclosed a number of difficult taxonomic problems in the Piperaceae, Chloranthaceae, and Moraceae families. Herbarium studies indicated that there were very closely related taxa in a number of genera. These closely related taxa could be interpreted either as species complexes or as single variable species. Field work in Costa Rica showed that many of these closely related taxa do not grow together. They may grow in the same general geographic area, but these closely related populations are usually found in different habitats or at different altitudinal levels. These observations have been very important in making taxonomic decisions, but they may also be important in recognizing processes of population differentiation and speciation in the wet tropics.

Delimitation of taxa in the neotropics is often based on rather few herbarium collections with little biological or ecological data. Such is the case in this study where estimates of affinity are based primarily on similarity or dissimilarity in vegetative and floral characters. Palynological, cytological, or biochemical data are not presently available for these species.

The data are based on plants collected in Costa Rica and the adjacent provinces of western Panama. While this may seem to be a very small area from which to make general speculations, it is rather well sampled when compared to other wet tropical areas. Not only does the area of Costa Rica and westernmost Panama have the benefits of decades of botanical exploration, but it also represents an area of isolated highlands with considerable endemism. This area is a minor but natural phytogeographic region, though its lowland species are often widespread.

Despite the small area there is a great altitudinal range (0–3800 m) and the patterns of rainfall are very different in different parts of the region. The deciduous forest formations of the northern Pacific lowlands can have less than 20 mm of rainfall during the dry season (December through April), while on the Caribbean side of the mountains, as little as 30 km away, the rainfall averages over 50 mm in the driest month of the year. However, the rainfall data alone can be misleading, especially at higher elevations. Turrialba on the Caribbean slope has an average annual rainfall of around 2400 mm, not much greater than some areas on the Pacific slope, such as Puriscal. The dry season on the Pacific slope, however, is much more severe and lacks the frequent cloudiness and misting of Turrialba and the Caribbean slope. These seasonal differences in cloud-cover and in rainfall affect the vegetation, and one can
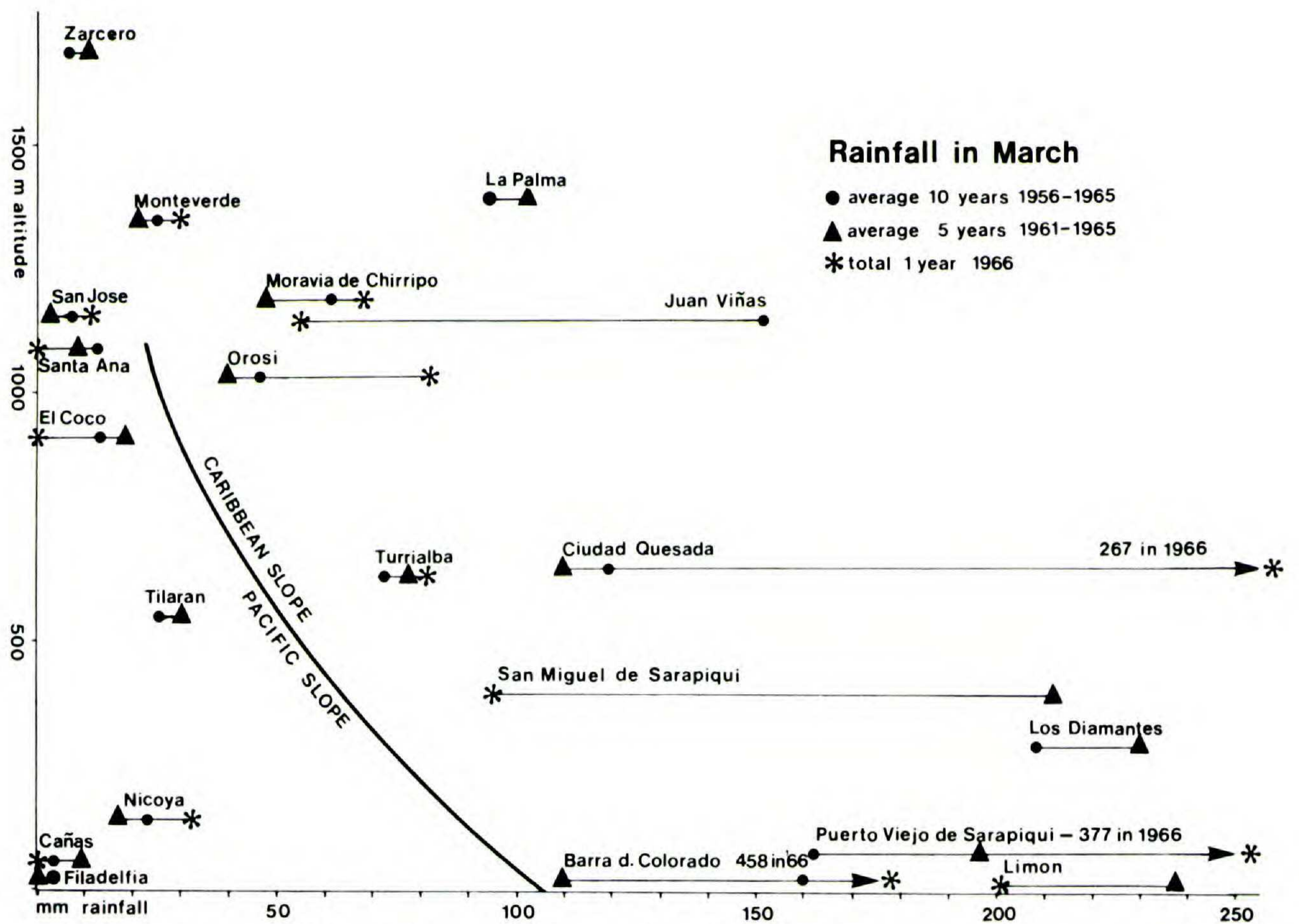
FIGURE 1. Rainfall in March at various altitudinal levels on the Caribbean and Pacific slopes of central and northern Costa Rica. The ordinate represents altitude in meters. The abscissa presents rainfall in millimeters for the month of March in the latter half of the dry season.

see striking differences over a distance of only a few kilometers in some areas. Relative humidity and evaporation data are not available. These would be more meaningful than simple rain-gauge readings.

An understanding of the topography and rainfall patterns is essential to any analysis of species distributions in Costa Rica. The life-zones depicted in the *Mapa Ecologico* (Tosi, 1969) give a good representation of the kinds of vegetation to be found in Costa Rica. However, precise use of the life-zone system is very difficult with museum specimens collected over a hundred-year period. Instead, I have used altitude and slope based on the geographical data found with the specimens to estimate the kind of environment in which the material was collected. By graphing altitude (ordinate) against rainfall in March at the height of the dry season (abscissa) it is apparent how different the Caribbean and Pacific slopes are (Fig. 1) in northern and central Costa Rica. (The Pacific slope of southern Costa Rica receives much more rainfall than the northern half and is not included in these graphs.) The plant collections are primarily from these same areas, and the resultant figures of distribution may not hold true for a few of these species which grow in other areas of Central America. The purpose of the graphs is simply to show how some closely related species are separated by altitude and slope in Costa Rica. The graphs are based on rainfall data from the *Anuario Meteorlogico 1966* (1967) of the Servicio Meteorologico Nacional of Costa Rica.
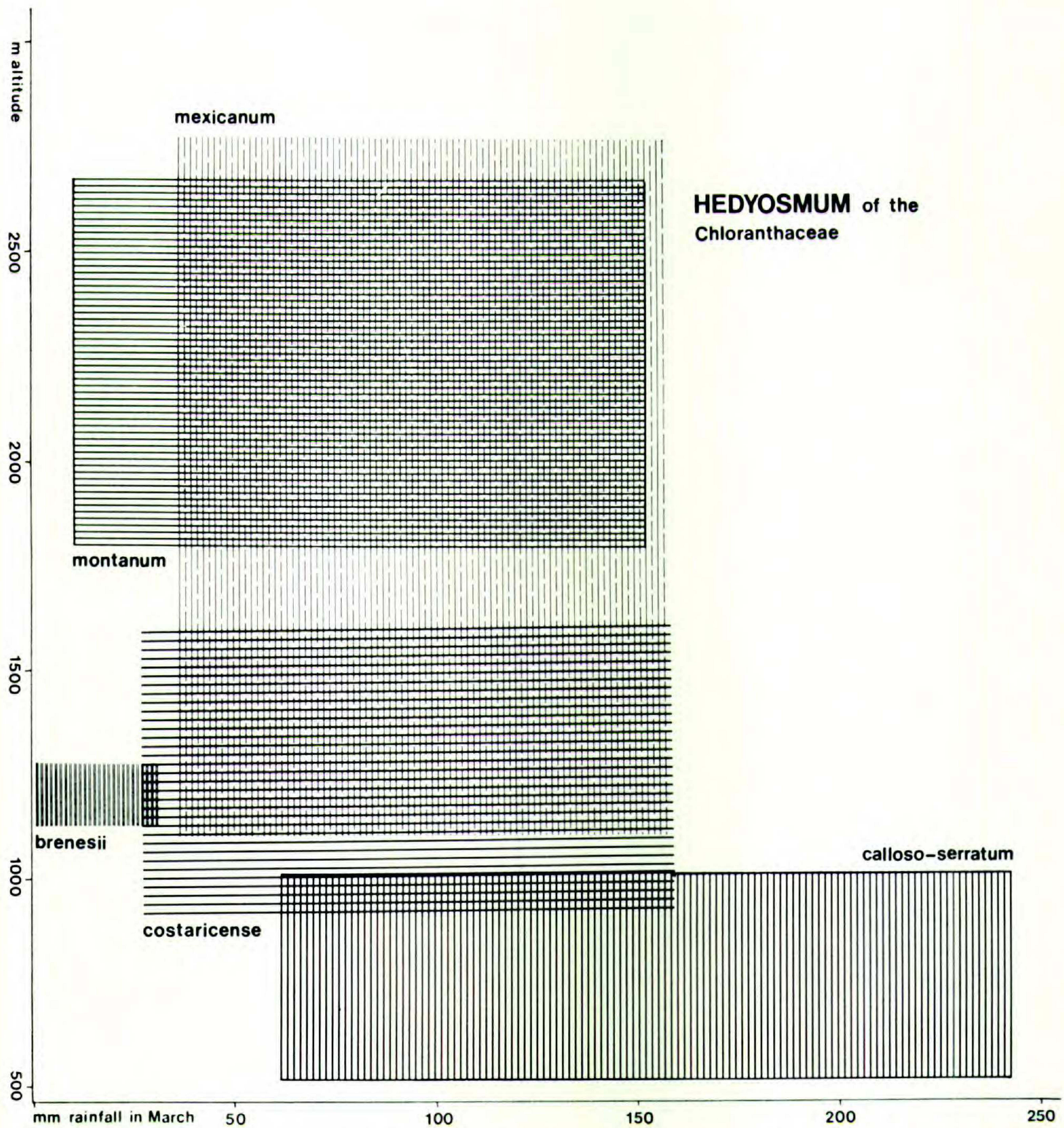
FIGURE 2. Distribution of the species of *Hedyosmum* in Costa Rica plotted against altitude in meters (ordinate) and rainfall for March in millimeters (abscissa). The boxed areas of *H. montanum* and *H. calloso-serratum* represent plants that were thought to be conspecific.

OBSERVATIONS

The genus *Hedyosmum* of the Chloranthaceae presents a series of distributions that is characteristic of many genera in Costa Rica (Fig. 2). These distributions are characterized by the fact that the very different species (from a morphological point of view) often share the same habitat, while those that appear to be very similar and were even thought to be conspecific do not grow together. *Hedyosmum mexicanum* Cordemoy, with its capitate female inflorescence, is the most easily distinguished species in Costa Rica. It ranges from 1100 to 2800 m elevation in many of the same habitats as *Hedyosmum montanum* Burger and *H. costaricense* Wood. *Hedyosmum costaricense*, with leaves having many secondary veins, is likewise easy to identify and shares
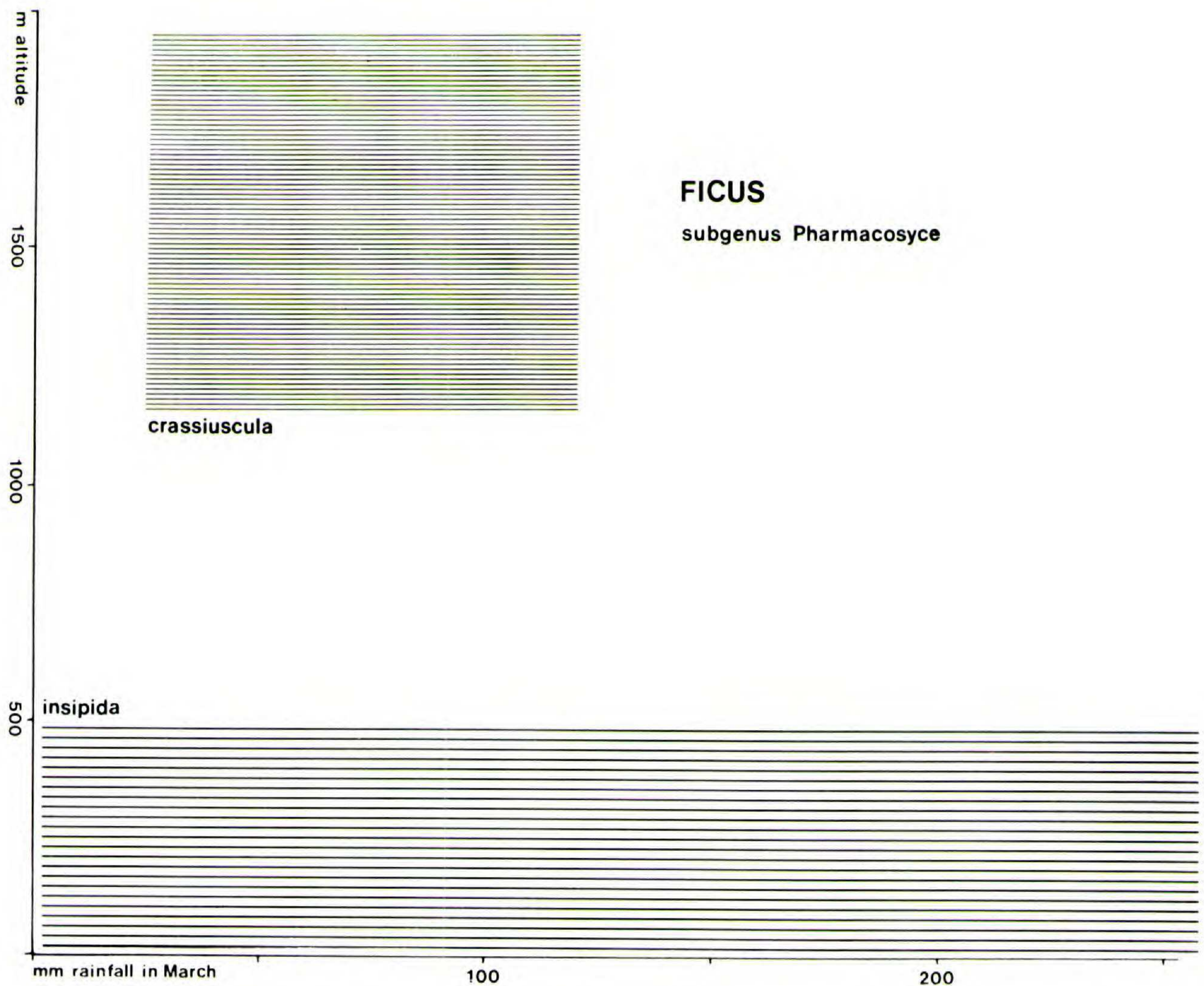
FIGURE 3. Distribution of *Ficus crassiuscula* and *F. insipida* in Costa Rica, plotted against altitude in meters (ordinate) and rainfall in March (abscissa).

some of its habitat with two other species of the genus in Costa Rica. *Hedyosmum brenesii* Standley is unusual in having monoecious plants and shares a small part of its range with *H. costaricense*. Material that is here referred to two species, *H. montanum* and *H. calloso-serratum* Oersted, was long referred to a single species: *H. calloso-serratum*. In Costa Rica, after over a hundred years of botanical collecting, we still lack material of either of these two closely related species in the altitudinal range of 1000 to 1800 m, though together they range from 500 to 2800 m elevation. The differences between the two taxa are subtle but consistent and correlate with their separate distributions. These two species are closely related to *H. scaberrimum* Standley of western Panama, and the relationships of these three species in that area are not clear because of the paucity of collections. It may be that the three form a complex or *artenkreis* with only the more differentiated extremes reaching central Costa Rica. In any event, in Costa Rica the most closely related taxa of this genus do not grow together.

Examples of very closely related species that do not share the same habitat can also be found in *Ficus* of the Moraceae. DeWolf authored the treatment of *Ficus* in the Flora of Panama (Woodson and Schery 1960) and Woodson, who had also surveyed the species, was in close agreement with DeWolf's species
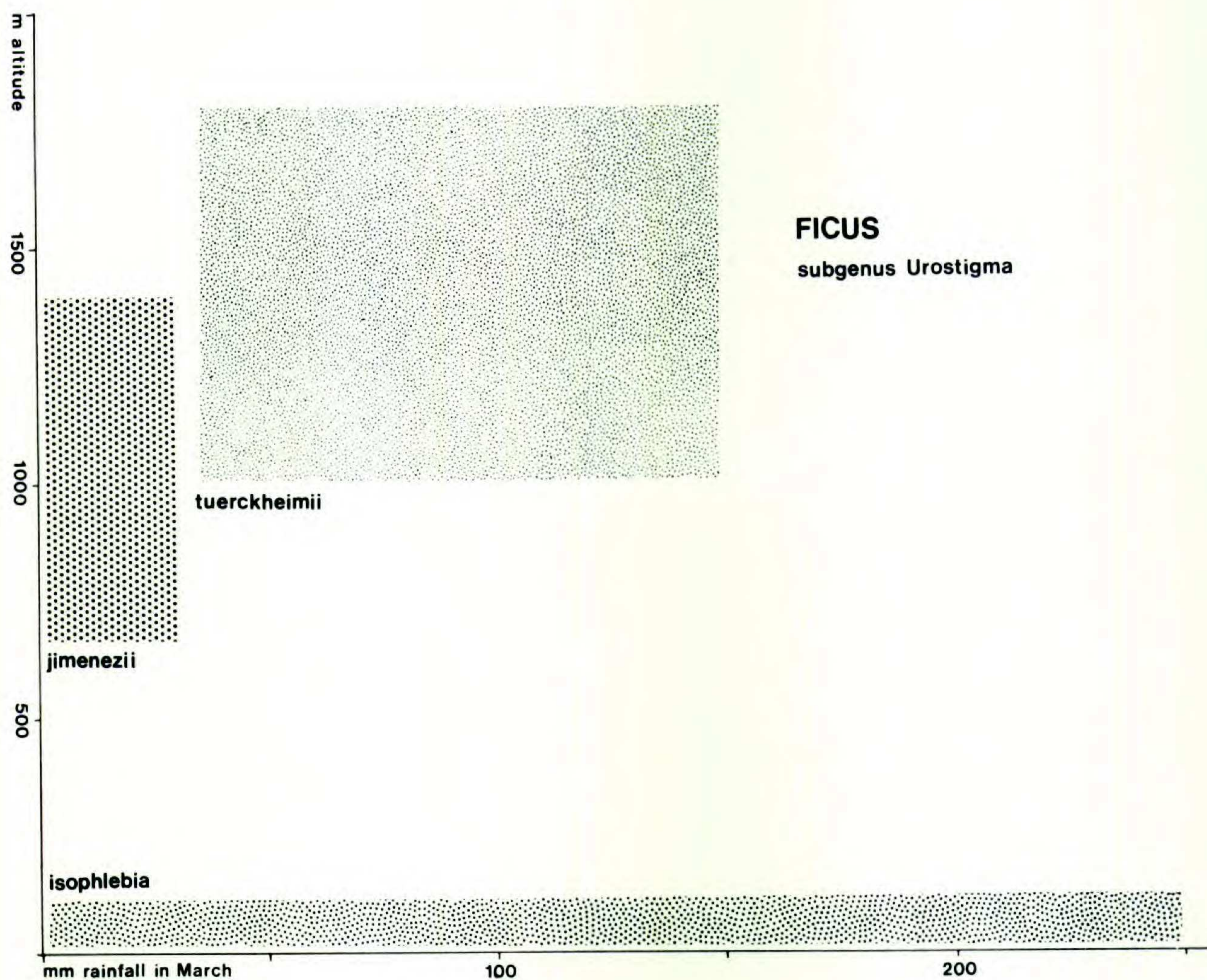
FIGURE 4. Distribution of *Ficus isophlebia, F. jimenezii,* and *F. tuerckheimii* in Costa Rica plotted against altitude in meters (ordinate) and rainfall in March (abscissa).

delimitation. In the decade since that treatment was published some species have come to be known by twice as many collections as were previously available. Most of the species-concepts delimited in the *Flora of Panama* (Woodson & Shery, 1960) have held up well under the scrutiny of the new material, but a few appear to have been made too broad. There are two such groups, one in each of the two subgenera. In the subgenus *Pharmacosyce, Ficus crassiuscula* Warburg was placed into synonymy under the wide-ranging *F. insipida* Willdenow. Close examination of material referable to *F. crassiuscula* shows that it grows only above 1100 m in Costa Rica and western Panama. While in our area, *F. insipida* has not been collected above 500 m elevation (Fig. 3). In the subgenus *Urostigma,* DeWolf considered a trio of names synonymous: *F. isophlebia* Standley, *F. jimenezii* Standley, and *F. tuerckheimii* Standley. Plotting the known collections of these three species in our area shows again that they do not share the same habitat (Fig. 4). William Ramirez has shown (1970a) that *F. isophlebia, F. jimenezii,* and *F. tuerckheimii* have different species of pollinators as do *F. insipida* and *F. crassiuscula.* Dr. Leslie Holdridge, a forest ecologist who knows these plants in the field, recognizes all as distinct (personal communication). The work of DeWolf, however, points out the very

close relationships of these species. Here again, as in *Hedyosmum*, the very closely related species do not live in the same habitat.

In the genus *Sorocea*, also of the Moraceae, there are four species in the area of Costa Rica and western Panama. *Sorocea cufodontisii* Burger is very closely related to S. *pubivena* Hemsley and is endemic to the wet evergreen lowland forests of southern Costa Rica and adjacent Panama in the Pacific lowlands. A reexamination of my earlier concept of S. *pubivena* (Burger *et al.*, 1962) leads me to believe that it does not grow along the Pacific slopes in this area. These two species are thus isolated geographically by the central mountain ranges. *Sorocea trophoides* Burger is also closely related to S. *pubivena* but occurs at higher elevations. *Sorocea affinis* Hemsley, which grows in some of the same areas as S. *pubivena*, differs more from that species than the others and may be adapted to sites of better drainage. Again, the pattern is similar: the more closely related species do not grow in the same general habitat, more distantly related species do.

These patterns of congeneric distribution are best seen in genera with many species. This is the case in *Piper* with about 93 species in Costa Rica and western Panama (Burger, 1971). One particularly difficult complex of closely related taxa is that of *Piper hispidum* Sw. and its allies. From an analysis of herbarium material it was evident that there was a pattern of associated morphological characters, but the differences between these taxa were very subtle and seemed to be unimportant. I postulated that different populations were slightly different morphologically and all together formed a mosaic complex with some local differentiation. I also assumed that these were all plants of forest edges and similar open habitats. My hypotheses, however, proved quite incorrect after study in the field—Some of these taxa were found only on the darkest forest floor, while others grew at the open forest edge. The subtle morphological differences were consistent and were correlated with geography and ecology and, more important, many of these very closely related taxa did not grow together nor could I find intermediate plants or intermediate populations. For this reason my complex of scarcely distinguishable populations were recognized as biological units defined by subtle but consistent morphological traits correlated with specific habitats.

These examples in *Piper* are not as clearly separate as are the examples from *Hedyosmum*, *Ficus*, and *Sorocea*. The simple charts used here would not distinguish some of these closely related species of *Piper* because they are, in part, separated geographically.

The very closely related genus *Pothomorphe*, often considered synonymous with *Piper*, is represented by two species in Costa Rica. *Pothomorphe peltata* (L.) Miq. ranges from near sea level to about 700 m elevation, while *P. umbellata* (L.) Miq. ranges to 2000 m elevation and is only rarely encountered below 700 m. Both species are plants of open weedy sites in moist or seasonally wet areas.

DISCUSSION

The significance of these observations would be questionable were it not for the fact that these patterns occur in several unrelated groups. The Amentif-

erae (*sensu* Engler), to which they belong, are an admittedly artificial alliance of plant families. Many of these families are probably unrelated at the ordinal level. The Chloranthaceae and Piperaceae are probably related to the Ranales, while the relationships of Moraceae are thought to be with the Hamamelidales. The fact that genera in these unrelated families exhibit similar patterns of distribution as regards intrageneric morphological affinity is, I believe, significant.

An objection to the interpretations made here might be that the morphological differences used to separate taxa are ecologically induced and we are only dealing with ecotypes. If this latter interpretation were true, we would expect to see clines within the range of these species. *Hedyosmum montanum*, for example, ranges from 1800 to 2800 m elevation but is quite uniform throughout this range; likewise, the closely related *H. calloso-serratum* shows no ecologically correlated variation in its 500 to 1000 m range. In fact, the lack of clinal variation is a characteristic of many tropical species (Ashton, 1969). It is this lack of clinal variation together with relatively more uniform populations that allow us to identify these closely related taxa. (There are, of course, many tropical plant species that vary greatly. In the genera *Urera* and *Myriocarpa* of the Urticaceae variation is often so great that species delimitation is quite arbitrary and about 10% of the specimens cannot be identified with certainty.)

That all these examples might be interpreted as subspecies does not negate the thesis of ecological differentiation as an important factor in producing the great number of species to be found in the wet tropical forest. Whether species or subspecies, these taxa are presently separate. Evidence from *Ficus* suggests that some of these closely related taxa are, in fact, genetically isolated. Trees of *Ficus tuerckheimii* have been planted in the parks of San José, Costa Rica. This is about 15 km outside of the closest natural occurrence of the species and within the ecological range of *F. jimenezii* which grows in San José and the Meseta Central. William Ramirez (1970b) observed these trees of *F. tuerckheimii* for two years and found only six matured figs (syconia) during that time. They had been entered by one of the pollinating species of *F. tuerckheimii*. The pollinating wasps of *F. jimenezii* were never observed to enter the figs of *F. tuerck-heimii* despite the fact that these wasps occur in the area.

The species discussed and represented here have very precise and rather narrow ecological boundaries. Are these boundaries real? A great many species of the tropics do have wide ranges and they do not seem to have such precise boundaries. Our question concerns only a small percentage of closely related species. Some of these taxa are rare as evidenced by the poor representation in herbaria which may be giving us a false concept of their ecological amplitude. The smaller trees and shrubs such as *Piper* and *Hedyosmum* are much better represented in collections than the larger trees such as *Ficus*. Of Costa Rica's 93 species of *Piper*, 34 have an altitudinal range of less than 900 meters. In the case of *Hedyosmum montanum* we have 14 collections representing 11 collection areas. Of these, four areas range between 2100 and 2800 m altitude with the remaining seven areas from between 1800 and 2100 m. In *Hedyosmum calloso-serratum* (in a narrow sense) we have 21 collections representing 15 areas. Of these, 11 areas are between 600 and 1000 m elevation and four areas from 500

to 600 meters. At the lower elevations at least, the samples fall off sharply, though these lower areas have been frequently visited by collectors. Thus, while sharp altitudinal and ecological boundaries may not be common, they are a real phenomenon in some species and do not appear to be an artifact of poor collecting.

How do these species maintain precise boundaries when their disseminules must certainly be transported over considerable distances and well beyond the population's perimeter? This question is especially interesting in *Ficus* subgenus *Urostigma* where most species begin as epiphytes by having their sticky seeds transported by animals. Why is it that we have no collections of *Ficus tuerck-heimii* from the seasonally drier areas around San José in the area of *F. jimenezii*? Trees of *F. tuerckheimii* planted in San José show that the species can grow and mature outside of its native habitat. The pollinating wasps reached these trees so that mature seeds were set (Ramirez, 1970b). The only answers that suggest themselves are in the areas of seedling mortality and competitive exclusion in early stages of growth. There are no data available to support or deny these suggestions.

I do not wish to give the impression that closely related taxa never grow together but rather that this is an exceptional situation. In *Piper* a closely related complex of species (*P. biseriatum* C. DC., *P. cenocladum* C. DC., *P. fimbriulatum* C. DC., *P. imperiale* (Miq.) C. DC., and *P. obliquum* R. & P.) often grow together on the dark floor of wet lowland evergreen forests.

The observations presented in this paper contradict the generalization of Federov (1964) that the tropical wet forest possesses series of closely related species growing together. The Costa Rican material indicates that though closely related species appear to grow within the same small geographic area they do not usually grow together within the same habitat. Species of birds that are very closely related and cannot invade each other's territory have been called parapatric sister species (Mayr, 1969).

The evidence of closely related parapatric plant species in Costa Rica can be most easily explained by assuming that effective genetic isolation has evolved over relatively small geographical distances. The alternative is to postulate archipelagos, refugia, or similar devices providing larger scale geographic isolation. Costa Rica's small area (equivalent to the State of West Virginia) and its very diverse epiphytic flora argue, I believe, against major climatic or geological changes in the recent past.

Costa Rica is well known for the richness of its orchid flora with over a thousand species. This extraordinary diversity is found in other epiphytic plants representing a wide range of families. Diversity in plants especially sensitive to desiccation implies that there have been no major contractions of Costa Rica's wet forest formations in the recent past. The central mountain chain provides some isolation between the Caribbean and Pacific slopes. The Pacific lowlands of northern Costa Rica have a very severe dry season and support a vegetation different from that found elsewhere in the country. The Pacific lowlands of southern Costa Rica have a much less severe dry season, and this area supports evergreen forest. There is considerable endemism in this part

of Costa Rica, from about the western slopes of the General Valley to the Osa Peninsula and the highlands of Chiriquí, Panama. The Caribbean slopes and lowlands are more uniform as regards climate, and the vegetation is essentially continuous. The areas of higher altitudes are rather small and perhaps insufficient in area to support theories of refugia during major climatic changes. I prefer to assume that major fluctuations in sea level or climate have not contributed significantly to the plant diversity of Costa Rica. Most of the species discussed previously in this paper are endemic to Costa Rica and adjacent Panama, and I believe they have arisen without the influence of major geological or climatic events.

If refugia did exist and did provide large scale geographic isolation for the development of these closely related species, other equally puzzling questions arise. Why do these species remain separate yet closely adjacent after the postulated isolation? And how is it that this isolation produced two species differing so precisely in their ecological requirements? The hypothetical climatic and geographic changes necessary for large-scale isolation raise as many serious questions as they attempt to solve.

Unfortunately, we are only describing an assumed phenomenon. Our interpretations are based on the assumptions that our samples are large enough and that our morphological taxa do indeed represent genetically isolated populations. If these interpretations are valid, we are faced with a situation which can be simply explained by a very hypothetical process: speciation or the initiation of genetic isolation over very small (10 km) distances. Ecological and genetic studies in the land snail *Partula taeniata* suggest that striking divergence can take place between adjacent populations in the absence of geographical barriers (Clarke & Murray, 1969). The plants discussed here do not lend themselves to genetic analysis but they exhibit some of the same phenomena seen in *Partula*. Additionally, biologists may have overemphasized the effect of gene flow on the processes of population differentiation (Endler, 1973).

The relative rarity of hybridization and clinal variations, the great number of species with relatively uniform populations, and the frequency of species with narrow ecological boundaries reflect an evolutionary strategy common in the wet tropics. We are most familiar with plants of environments with wide climatic fluctuations. In these genetic diversity or adaptive pliability is probably more important than adaptive precision. In a very uniform environment precision of adaptation, I believe, is more often a successful strategy. Chance and biological parameters, more than temperature and rainfall, determine reproductive success. Janzen (1967) has ably discussed the higher fidelity of animals and plants to spatial and temporal habitats set off by minor differences. In these more uniform environments it is adaptation to a particular habitat that may determine survival and not the ability to withstand a set of extremes. It is in this context that speciation over small distances in areas of ecological gradients appears to take place. While we may not understand how genetic isolation has been achieved over these small distances, I believe that the evidence from very closely related parapatric plants species indicates that speciation has indeed occurred over small distances in Costa Rica.

SUMMARY

A number of problems involving very closely related species in several genera of Costa Rican flowering plants have been resolved because, though almost sympatric, the species actually do not grow together. These parapatric sister-species or species-groups are found in unrelated families and may represent a general phenomenon. A simple explanation for the origin of these closely related species-pairs and species-groups is that they have become adapted to slightly different habitats and that this has provided small but effective spatial isolation. It seems possible that under the selection pressures found in the wet tropics relatively short periods of isolation and equivalently small distances may be sufficient to develop new co-adapted gene complexes. In turn, these may be easily destroyed by hybridization with the result that gene-flow between formerly sympatric and interbreeding, but now separate, populations quickly becomes detrimental to both. This provides a simple explanation, without refugia and without major geological changes, for these ecologically isolated, morphologically only slightly different taxa that show no evidence of gene-exchange.

LITERATURE CITED

ASHTON, P. S. 1969. Speciation among tropical forest trees: some deductions in the light of recent evidence. Biol. Jour. Linn. Soc. 1: 155–196.

BURGER, W. C. 1971. Flora Costaricensis, Piperaceae. Fieldiana: Bot. 35: 5–227.

————, J. LANJOUW & J. G. WESSELS BOER. 1962. The genus *Sorocea* St. Hil. Acta Bot. Neerl. 11: 428–477.

CLARKE, B. & J. MURRAY. 1969. Ecological genetics and speciation in land snails of the genus *Partula*. Biol. Jour. Linn. Soc. 1: 31–42.

ENDLER, J. A. 1973. Gene flow and population differentiation. Science 179: 243–250.

FEDEROV, A. A. 1964. The structure of the tropical rain forest and speciation in the humid tropics. Jour. Ecol. 54: 1–11.

JANZEN, D. 1967. Why mountain passes are higher in the tropics. Amer. Naturalist 101: 233–244.

MAYR, E. 1969. Bird speciation in the tropics. Biol. Jour. Linn. Soc. 1: 1–17.

RAMIREZ, W. 1970a. Taxonomic and biological studies of neotropical fig wasps. Univ. Kansas Sci. Bull. 49. 44 pp.

————. 1970b. Host specificity of fig wasps. Evolution 24: 680–691.

TOSI, J. A., JR. 1969. Republica de Costa Rica, Mapa Ecologico. Centro Cientifico Tropical, San José.

WOODSON, R. E. & R. W. SCHERY. 1960. Flora of Panama. Ann. Missouri Bot. Gard. 47: 146–165.